

PATTERNS OF DISTRIBUTION AND ABUNDANCE IN
SMALL SAMPLES OF LITTER-INHABITING ORTHOPTERA
IN SOME COSTA RICAN CACAO PLANTATIONS

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Abstract.—Collections of Orthoptera and Dictyoptera associated with rotting organic litter in cacao plantations at three localities in Costa Rica are described. These collections, in which the Blattodea were the most represented, were taken from experimental, replicated treatments of rotting discs of banana tree trunks placed on the ground, piles of natural leaf litter on the ground, and arboreal leaf litter contained in large plastic cups suspended from the lower branches of cacao trees. For two localities, there was one collection each for the lengthy rainy season and the short, erratic dry season; only one rainy season collection was taken at the third locality. The most abundant cockroach was *Latiblatta* sp., occupying arboreal litter samples at all three localities followed by *Eurycotis* sp. which occupied both arboreal and ground litter microhabitats at one locality only. Most of the other taxa were represented by one individual at one locality only, suggesting very patchy distributions, assuming an adequate sample size. At one locality (La Lola), the tettigoniid *Idiarthron hamuliferum* Beier was found in arboreal litter, as was a leaf-rolling cricket, *Camptonotus* sp. prob. *affinis*. Most orthopterans were found in litter associated with sunny areas of cacao during the dry season, a probable response to seeking refuge in the few available moist patches, whereas numbers and densities were always lower in the well-shaded areas in both rainy and dry periods. The arboreal leaf litter microhabitat in tropical forests deserves particular attention for understanding the vertical stratification of cockroach faunas.

This paper summarizes some preliminary field data on the association of Orthoptera (Tettigoniidae and Gryllacrididae) and Dictyoptera (Blattodea) with several kinds of rotting organic litter substrates, "microhabitats," in cacao plantations at three localities in Costa Rica. The information gathered in this study was adjunct to an investigation of the occurrence of immature stages of cacao-pollinating Diptera in these litter substrates (Young, 1982, 1983). Orthoptera and Dictyoptera are commonly associated with the cacao plantation habitat overall, although seldom are they of any economic importance (e.g., Leston, 1970). The major group discussed in this paper, the Blattodea or cockroaches, represent only about 10 percent of the total cockroach fauna described for Costa Rica (see the review of Fisk, 1971). Nevertheless, the data are new in terms of both describing cacao plantations in

the Neotropical Region as Orthoptera and Dictyoptera habitats, and the observed patterns of specificity for some of the forms collected.

METHODS

Between 1978 and 1980, replicated series of field "treatments" consisting of increased abundance of three kinds of natural litter substrates, were distributed in cacao (*Theobroma cacao* L.) plantations at three localities or collecting sites in Costa Rica (see Young, 1982, 1983 for descriptions of these sites and studies). The localities are: (1) "Fincas La Tigra and El Uno," near La Virgen (10°23'N, 84°07'W), Heredia Province, (2) "Finca Experimental La Lola," near Siquirres (10°06'N, 83°30'W), Limon Province, and (3) "Turrialba or CATIE," Turrialba (9°54'N, 83°41'W), Cartago Province. These localities are within Lower Montane Tropical Wet Forest (Turrialba), Premontane Tropical Wet Forest (La Tigra and El Uno), and Lowland Tropical Wet Forest (La Lola) regions (Holdridge, 1967). Each locality experiences a short, irregular dry season each year (Fig. 1), during which the ground leaf litter in sunny areas of cacao plantations (areas with a broken or poor canopy cover of shade trees) becomes dry and crunchy underfoot.

The La Tigra and El Uno cacao is about 10–15 years old, with the La Tigra plantation having a broken canopy of natural tree species from regenerating trees establishing very shaded conditions. The La Lola cacao plantation area studied consists of the UF-29 variety (La Tigra and El Uno is mixed varieties) shaded primarily by *Erythrina* and other Leguminosae, and with one area (A) with heavy shade (shaded habitat) and another (B) with less shade (sunny habitat) throughout the year. The La Lola cacao trees are 20–30 years old. The Turrialba plantation area studied consists of "Catongo" variety trees with a highly variegated canopy establishing both shaded and sunny areas. Cacao trees here are 20–30 years old.

The three kinds of organic litter substrates studied are: 2 × 2-meter ground plots of piled leaf litter (mostly cacao leaves), 22-meter ground plots of discs of banana tree trunks, and 200-cm²-leaf-litter-filled plastic cups suspended in cacao trees. In addition, observations on Orthoptera, Dictyoptera, and other insects inhabiting piles of rotting cacao pods were also made.

For La Tigra and El Uno cacao plantations each, there are eight replicates of the "ground leaf litter" treatment, employing sturdy wooden frames to hold the litter in place beneath the cacao trees. There are also eight replicates of the rotting discs of banana tree trunks in each of the two areas, as well as twenty plastic cups, the "arboreal leaf litter" treatment in each area. The same distribution of treatments is also used for Areas A and B at La Lola (Figs. 2–4). The rotting discs of banana tree trunks treatment consists of 20–30 discs per replicate renewed approximately every 3–4 months. The plastic cups used for the "arboreal leaf litter" studies (Fig. 3) have perforated bot-

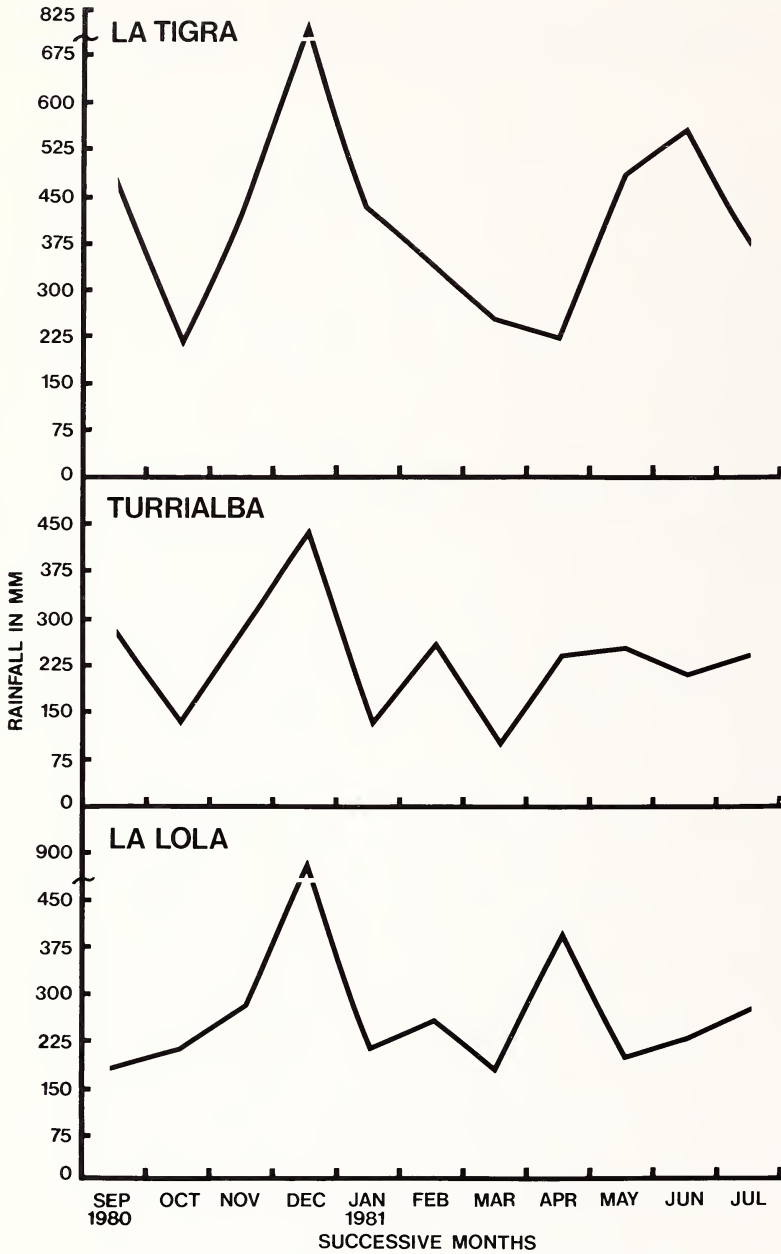


Fig. 1. Monthly patterns of rainfall at three cacao-growing localities in Costa Rica during 1980 and 1981. There is a depression in rainfall during the January–February period at these localities, most evident at the La Lola and Turrialba localities. All three regions, however, are classified as relatively non-seasonal compared to other tropical regions with a very pronounced dry season each year.



Fig. 2. The La Lola cacao plantation, near Siquirres, in Limon Province, Costa Rica. Top: general view of the “sunny habitat” (Area B). Below: ground litter in the shaded habitat (Area A). Note wooden frame filled with leaf litter in the left foreground.



Fig. 3. Ground leaf litter treatment used to assess litter-inhabiting Orthoptera. Top: typical positioning of one replicate beneath a cacao tree. Below: typical distribution of cacao leaf litter in wooden frame. Photographs taken at La Lola during the "dry" season. Note great abundance of leaves in the wooden frame at this time.

toms to allow drainage of rainwater. The cups are suspended by sturdy wires from lower branches of individual cacao trees. A pattern of randomization was used to position treatment replicates in La Lola and Turrialba. For La Tigra and El Uno, a different system was used, one in which replicates were placed in distinctive-appearing sub-areas. Whenever the litter substrates were collected for sampling of insects (see Young, 1982, 1983), fresh litter was added from the same general areas of the plantations to continue the treatments. Further details and descriptions of the treatments are given elsewhere (Young, 1982, 1983).

For the rotting discs of banana tree trunks (Fig. 2), prepared by slicing freshly fallen banana trees with a machete and allowing the discs to rot for several months, field notes were taken on the approximate numbers of insects seen scurrying off when discs were collected in plastic bags for sorting of insect material in the laboratory. Additional notes were taken only on an opportunistic basis for orthopterans that scurried off in the laboratory. For the ground and arboreal leaf litter treatments, however, virtually all of the orthopterans that were found in the individual substrates were collected. It is emphasized that the samples were taken during the daylight hours, a period when many orthopterans were concealed in the litter substrates being studied.

Collected orthopterans were preserved in 70 percent ethanol for subsequent determinations. The litter samples were always collected by placing the contents of a substrate container (wooden frame or cup) into a plastic bag and tying the bag shut. Orthopterans less than 5 mm long were either missed or not collected. For La Tigra and El Uno, there was one major collecting period or sample, August 1980, the mid-rainy season. For La Lola and Turrialba, however, samples were taken in both the late rainy season (November 1980) and mid-dry season (February 1981). In addition to these collections of Orthoptera and Dictyoptera, field observations on the occurrence of these insects in these substrates were made at several other times, although systematic collections were not made.

There is a lapse of at least four months from the time any of the substrates were initially disturbed after being set up. The substrates were sampled several times within the time period of the present study, since they were used to estimate the abundance of cacao-pollinating Diptera (Young, 1982, 1983, and unpubl. data). Interest in the Orthoptera focused upon the comparison of ground and arboreal leaf litter as microhabitats, and relative changes in the estimated abundance of these insects in the rotting discs of banana tree trunks between rainy and dry periods (for La Lola in particular).

RESULTS

For all three collecting sites combined, more than three times the number of orthopteran individuals were collected from arboreal leaf litter than from ground leaf litter in cacao plantations, although number of species in each



Fig. 4. Top: arboreal leaf litter replicate, with forceps for scale. Below: rotting disc of banana tree trunk which forms a suitable microhabitat for roaches throughout the year, particularly during the dry season. Even though such substrates represent a combined area far less than the

kind of microhabitat was similar (Table 1). By far, the most abundant group, in terms of species and numbers of individuals in samples, were members of the Blattaria or cockroaches (Dictyoptera, Blattellidae) (Table 1). Most of the blattids represented in the limited samples from arboreal and ground leaf litter were nymphs, and one genus, *Latiblatta*, dominated the arboreal samples (Table 1). In some instances, individual roaches jumped from the cups when the litter samples were being collected, although this error is estimated at less than 10 percent for all samples.

Of particular interest was the discovery of several individuals of a leaf-rolling cricket, *Camptonotus* sp. prob. *affinis* Rehn, in a few of the arboreal litter samples from Area B (sunny habitat) at La Lola (Fig. 5). This species, along with the tettigoniid *Idiarthron hamuliferum* Beier (Fig. 5), were the only two orthopteran species encountered in the study. For both species, adults were found hiding beneath the dry leaves in the cups. *Camptonotus* specimens formed tubular nests from dead, dry cacao leaves within the cups. In addition, a single individual of *I. hamuliferum* was collected from its hiding place in thick moss in the trunk of a cacao tree at El Uno during the rainy season (July 1981). Both orthopterans were conspicuously absent, however, from cups and ground leaf litter collections at both La Tigra and El Uno throughout the study. Furthermore, both *Camptonotus* and *I. hamuliferum* were absent from all arboreal and ground leaf litter samples in Area A (shaded habitat) at La Lola for the entire study period. Thus, these forms were most abundant, albeit small samples, from the sunny habitat at La Lola and the mixed shade and sunny habitats in the cacao at Turrialba (the latter for *Camptonotus* only).

During both rainy and dry season samples at La Lola, roaches were very low in abundance in the arboreal leaf litter samples from Area A, the shaded habitat. Usually only 1–2 cockroaches were seen scurrying out of individual cups at both times, and with 60–100 percent of the cups without roaches at all. The leaf litter in these cups, as compared to that of the more exposed cups in Area B (sunny habitat), was always very damp and water-logged. In the arboreal samples from the sunny habitat, however, the cups with most individuals of cockroaches had dense layers of dry cacao leaves. During the dry season in Area B, between 80–100 percent of the cups had 1–5 roaches in each, whereas during the rainy season sample, only about 50 percent of the cups had cockroaches and occupied ones with 1–2 cockroaches each. A similar pattern was also found at Turrialba between dry and rainy season samples.

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leaf litter treatments used, densities of insects such as roaches are generally far higher in discs than other treatments, with this effect most noticeable in the dry season in sunny cacao habitats (La Lola).

Table 1. The daytime distribution and abundance of Orthoptera in arboreal ground leaf litter in Costa Rican cacao plantations.¹

Species	No. localities represented	No. individuals in arboreal litter	No. individuals in ground litter	Totals
Dictyoptera, Blattellidae				
<i>Latiblatta</i> sp.	3	26 (12A, 14N) ²	0	26
<i>Eurycotis</i> sp.	1	7 (N)	5 (N)	12
<i>Ischnoptera panamae</i> Hebard	1	1 (A)	0	1
<i>Blattella germanica</i> (L.)	1	0	1 (A)	1
<i>Anaplecta domestica</i> Saussure & Zehntner	1	0	1 (A)	1
"Undetermined Blattidae"	1	1 (N)	5 (N) (2 spp.)	6
Tettigoniidae, Pseudophyllinae				
<i>Idiarthron hamuliferum</i> Beier	2	2 (A)	0	2
Gryllacrididae, Gryllacridinae				
<i>Camptonotus</i> sp. prob. <i>affinis</i> Rehn	2	5 (A)	1 (A)	6
Total orthopterans by "micro-habitat"		42	13	57
% nymphal Blattidae in samples		52.4%	76.9%	56.1%
No. of "species"		7	6	10

¹ Data are combined for three cacao plantation collecting sites or localities and "no. localities represented" column indicates the localities at which specimens were collected. The three localities are: "Fincas La Tigra & El Uno" (considered as one site); "Finca Experimental La Lola"; "Turrialba or CATIE." See text for descriptions of these sites. For "La Tigra & El Uno" site, only one rainy season collection was made; for other sites, one rainy season and one dry season collection was taken for each one.

² Data are broken down in parentheses for numbers of adults (A) and nymphs (N) in samples.

Most of the orthopterans collected in this study were found exclusively in the arboreal leaf litter samples, and most of these were found in the rainy season for all three localities combined (Table 2). The most geographically widespread form is a species of *Latiblatta* occurring at all three localities, even though it is an arboreal leaf litter "specialist." The terms "specialist" and "generalist" species are used in this paper to refer to distributional

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Fig. 5. Top: the leaf-rolling cricket *Camptonotus* sp. prob. *affinis* Rehn. Below: the tettigoniid *Idiarthron hamuliferum* after being dislodged from the leaf litter of an "artificial bromeliad" (plastic cup) used as a replicate of arboreal leaf litter treatment. Both of these orthopterans were



encountered occupying arboreal leaf litter replicates in the sunny cacao habitat (Area B) at La Lola.

Table 2. Locality, season, and "microhabitat" specialists and generalists' among Orthoptera found in arboreal and/or ground leaf litter in Costa Rican cacao plantations.

Species	Exclusively arboreal	Exclusively ground	Generalist in both	No. of localities	Active season(s)
<i>Latiblatta</i> sp.	X	0	0	3	rainy
<i>Eurycotis</i> sp.	0	0	X	1 (La Lola)	rainy & dry
<i>I. panamae</i>	X	0	0	1 (La Lola)	rainy
<i>B. germanica</i>	0	X	0	1 (La Lola)	dry
<i>A. domestica</i>	0	X	0	1 (Turrialba)	rainy
"Undetermined Blattidae"	0 (?)	0 (?)	X	3	rainy
<i>I. hamuliferum</i>	X	0	0	1 (La Lola)	rainy & dry
<i>C. sp. prob. affinis</i>	X	0	0	2 (La Lola & Turrialba)	rainy & dry

No. arboreal specialist species: 4

No. ground specialist species: 2

No. leaf litter generalist species: 2

No. geographically restricted species²: 5

No. geographically widespread species: 3

No. dry season specialist species: 1

No. rainy season specialist species: 4

No. of tropical season generalist species: 3

¹ The terms "specialist" and "generalist" are used in this paper to define probable patterns of ecological distribution within the very limited samples obtained in this study. Similar patterns may, or may not, exist in whole populations.

² A geographically (regionally) restricted species is operationally defined in this paper as one found in samples obtained for only one collecting site or locality, while widespread species are those found in two or more such localities.

patterns within the very limited samples, and it may be difficult to extrapolate to whole populations due to severe limitations of the samples. The data (Table 2), while limited, suggest that there is considerable ecological diversification within the Blattidae of the Neotropical Region in terms of microhabitat, geographical distribution, and active season.

The La Lola cacao plantation contained the greatest number of "species" of litter-associated Orthoptera, with 4–7 species, depending upon the maximal number of "undetermined Blattidae" in the samples. In contrast, only one species was found at La Tigra and El Uno, an obvious underestimate generated in part by the very limited sampling, while 2–4 species were found at Turrialba. In all cases, however, the data are taken as pronounced underestimates of the actual orthopteran faunas of cacao.

The fact that the cockroaches collected in this study may have different ecological roles in cacao plantations is reflected in part by the morphological differences used in noting them under field conditions. Thus *Latiblatta* sp. was a "large tan roach" with nymphs either 18–22 mm long (La Tigra and

El Uno, and Turrialba) or 7–22 mm long for La Lola. *Eurycotis* sp. was recognized as a “chocolate-brown fat cockroach” with nymphs 15–22 mm long (La Lola), while *I. panamae* is a “medium size dark brown cockroach” with adults about 13 mm long (La Lola). *Blattella germanica* is a “large brown cockroach” with body size of 25 mm for the adult (La Lola), and *Anaplecta domestica* is a “small dark brown cockroach” of 6-mm-long adults (Turrialba). There are also three forms of “undetermined Blattidae” recognized in the field samples: “small dark brown” nymphs (5–8 mm long) (Turrialba); “small sooty brown” nymphs (6 mm long) (all three localities); “small rusty brown” nymphs (7 mm long) (Turrialba). The two orthopteran forms are readily distinguishable in the field (Fig. 5).

Field counts of cockroaches scurrying from the rotting discs of banana tree trunks (Fig. 4) indicate some interesting patterns of distribution: (1) general numbers of cockroach individuals found in discs are very similar among the three localities or collecting sites; (2) during the dry season (La Lola and Turrialba samples), 2–3 species are found in individual discs, mostly nymphs within size range 4–20 mm, with 1–5 individuals per disc and about 80% of the discs with one or more roaches; (3) during the rainy season (all three localities), there are 1–2 species present in discs at each locality, with 1–2 individuals (mostly nymphs) per disc, and about 30–50 percent occupancy rate of discs; (4) during the dry season in a sunny cacao habitat (Area B at La Lola), there are many more cockroaches (1–3 species, and 1–10 individuals per disc) in discs, with an occupancy rate of 80–100 percent, than in the nearby shaded habitat (Area A). Cockroaches are least abundant in all disc samples during the rainy season at all localities.

During the dry season in a sunny cacao habitat (Area B at La Lola), similar numbers of cockroaches are found in the discs and arboreal leaf litter samples, while far fewer are found in the ground leaf litter at this time. Such differences are far less pronounced in the nearby shaded cacao, with an overall depression of roach numbers during both dry and rainy seasons. During the lengthy rainy season at all three cacao-growing localities, there is a profusion of ant colonies (Young, in manuscript) associated with the three kinds of litter microhabitats, while ant colonies are far less abundant in these places during the dry season. Orthopterans such as *Camptonotus* and *I. hamuliferum* are not found in rotting discs of banana tree trunks and ground leaf litter throughout most of all of the year. Orthoptera in general are far less abundant in piles of rotting cacao pod husks than they are in ground litter throughout the year at the three localities.

The dry season impacts upon the sunny cacao habitat by a marked decline in all arthropods on a per unit basis of ground leaf litter, while other substrates, such as arboreal leaf litter and rotting discs of banana tree trunks, may exhibit marked increases in arthropod densities.

DISCUSSION

During the tropical rainy season, optimal conditions for activity in litter-inhabiting insects may be more evenly distributed over the cacao habitat than during the dry season, and such an effect is most pronounced in sunny areas of cacao (see also Young, 1983, for a discussion of these effects). A partial or broken canopy over cacao during the dry season permits the ground litter to dry out more thoroughly and faster than in more shaded areas of cacao. The result is an increased period of environmental thermal or moisture stress to small organisms inhabiting the litter. The data in the present paper indicate that cockroaches and large-bodied Orthoptera that occupy leaf litter and other litter substrates (rotting discs of banana tree trunks) during the daylight hours in cacao plantations may become more abundant in arboreal litter microhabitats characterized by dense layers of dead leaves. Rotting discs of banana tree trunks become ecological "refuges" for small-bodied insects (less than 5 mm long) during the dry season, even in sunny cacao habitats (Young, 1983). Even though cockroaches in the tropics may be active nocturnally for feeding and courtship (e.g., Schal, 1982; Schal and Bell, 1982), the availability of moisture-holding microhabitats in cacao habitats provides a daylight shelter for hiding from thermally stressful conditions and deleterious biological factors such as predators. Given the large diversity of the Costa Rican cockroach fauna (Fisk, 1971), the observed patterns of different distributions in the small number of species studied here indicate that the group as a whole has undergone considerable ecological diversification in the Neotropical Region.

Assuming that the sample data are adequate to explain patterns of distribution in populations, it appears that most of the cacao cockroach fauna is arboreal in terms of litter microhabitat. Tropical cockroaches are considered as major converters of decaying litter to other nutrients (e.g., Irmiler and Furch, 1979). Some species, such as *Anaplecta domestica* Saussure and Zehntner, may be ecologically flexible in occupying both arboreal and ground litter. In the present study, this species was found in ground litter, although the related *A. mexicana* Saussure occurs in epiphytes in Costa Rica (Fisk, 1971). Such species, and the very common *Lattiblatta* sp. may be adapted to exploit litter and other litter-inhabiting organisms as food in natural epiphytes such as tank bromeliads as well as in the "artificial bromeliads" of arboreal leaf litter used in the present study. In a previous study of the daytime-foraging of insects at experimentally-placed food baits in the lower understory layer (at heights of 1–2 m) in lowland tropical rain forest ("Finca La Tirimbina," adjacent to "Finca La Tigra") and semi-deciduous wet forest ("Barranca Site, near Miramar, Puntarenas Prov.") in Costa Rica during the 1975 dry season (January–February 1975 collections), a total of 5 cockroaches (2 species) were collected from three bait-types (pineapple, orange,

and grape jelly) at Barranca at 0900 hours, one on pineapple at 1300, none at 1500, and a total of four on three bait-types (pineapple, jelly and ground beef) at 1700 hours (A. M. Young, unpubl. data). Only one cockroach foraged at one bait from 0900 to 1300 hours at La Tirimbina (Young, unpubl. data). Such data, involving replicated series of food baits along transects in forest understory, and in which large quantities of other insects were captured at baits, indicate the low activity level of roaches during these periods and times of the day.

The layers of dead leaves in the plastic cups most likely provide a suitable hiding site for *Camptonotus* and *I. hamuliferum* during the daytime, and feeding presumably occurs elsewhere, such as in the cacao canopy. *Camptonotus carolinensis* (Gerstaecker) is known to feed on scale insects in North American forests, and this species constructs rolled-leaf nests anchored with silk, using fresh, attached leaves of the tree (Blatchley, 1920). The use of dead cacao leaves by *Camptonotus* in the present study as a rolled-leaf nesting site represents a departure from the usual habit of using leaves on the host plant. The absence of *Camptonotus* sp. from the La Tigra and El Uno arboreal litter may reflect a difference in food preferences. The occurrence of bromeliad-festooned shade trees in both cacao habitats may provide a suitable dry-season refuge for these orthopterans, whereas at La Lola, at least *Camptonotus* sp. requires the artificial bromeliads as a refuge. Whether or not these orthopterans move each evening into the canopy trees for feeding remains to be studied.

The marked difference in abundance of orthopterans in the small samples between dry and rainy seasons, with most occurring in the rainy season samples for all localities, may reflect the complex fluctuations in the abundance of roaches and other foliage-dwelling insects in response to seasonal conditions in Central America (Wolda, 1978; Wolda and Fisk, 1981). Nymphal stages of roaches in particular exhibit marked cycles of abundance (Wolda and Fisk, 1981).

The lower densities of Orthoptera and other litter-inhabiting arthropods observed for cacao habitats with heavy shade and year-around moist conditions (see also Young, 1983) may be due in part to the more uniformly moist conditions of such areas and also to a greater abundance of predatory forms such as ants under these conditions. Shaded cacao habitats tend to accumulate a high number of ant species (Bigger, 1981). Orthoptera are more abundant in sunny cacao habitats (Bigger, 1981), as also observed for the Area B habitat at La Lola in the present study. Rotting discs of banana tree trunks may exhibit less of a water-loss response to the tropical dry season than less dense substrates such as dead cacao leaves. Under such conditions, insects inhabiting discs, both in sunny and shaded cacao habitats, may exhibit less of a response, in terms of density or shifts in numbers of species,

than insects in leaf litter. Young (1983) found that such discs provided a suitable refuge for the immature stages of cacao-pollinating Diptera (Ceratopogonidae) to pass the dry season at La Lola, particularly in the sunny habitat. Cacao leaf litter may represent a relatively more ephemeral microhabitat for many small-bodied insects, including the early instars of cockroach nymphs, in sunny cacao habitats, and particularly during the drier months of the year. Large-bodied insects such as bigger roach nymphs, adult cockroaches of some species, and other orthopterans (such as *Camptonotus* sp. and *I. hamuliferum*), may have little difficulty in occupying the semi-moist to dry arboreal leaf litter provided by the plastic cups in cacao trees. But during such periods, small-bodied insects, including ants, are virtually absent from such microhabitats. For those orthopterans that actually feed on the leaves of cacao trees, seasonal cycles in the availability of young leaves may greatly influence the abundance of these insects in cacao plantations (Majer, 1975). Tettigoniidae, for example, increase in abundance with the onset of flushes of cacao leaves in Ghana plantations (Majer, 1975). Cockroaches, being opportunistic feeders on a variety of food-types, may exhibit less regular fluctuations in abundance.

The foregoing discussion considers what might be the overall trends in relative abundance patterns, seasonal distributions, and daytime-resting places for a relatively small portion of the Costa Rican orthopteran fauna associated with cacao plantations. Given the type of sampling performed and the number of collection dates, the data are large underestimates of the probable fauna resident in such habitats. Had larger samples been obtained for longer periods of time, it might very well have been shown that individual taxa of Blattodea exhibit very flexible behavior in terms of daytime-resting sites. Thus, it would not be surprising to discover that most or all of the cockroach taxa discussed in this paper are "generalist" forms in terms of hiding in both arboreal and ground leaf litter. Yet given the tremendous vertical complexity of tropical rain forests (e.g., Richards, 1964), it would also not be surprising to discover that some of the taxa are, in fact, canopy or sub-canopy "specialists," occupying large epiphytes accumulating organic litter. Such effects must be taken into account when considering the relatively low vertical complexity of the cacao habitat, a condition that may alter the distribution of cockroaches that would otherwise be found in undisturbed tropical rain forests.

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